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Facultative mycorrhizal associations promote plant naturalization worldwide

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Abstract. Mycorrhizal symbiosis has received relatively little attention as a mechanism explaining plant naturalizations at a global scale. Here, we combined data on vascular plant species occurrences in over 840 mainland and island regions from the Global Naturalized Alien Flora (GloNAF) database with up-to-date databases of mycorrhizal associations. We tested whether the mycorrhizal type (arbuscular, AM; ectomycorrhizal, ECM; and non-mycorrhizal, NM) and status (facultative and obligate) were associated with two measures of naturalization success, (1) naturalization incidence (reflecting the ability to naturalize, and expressed as whether or not a plant species is recorded as naturalized anywhere in the world) and (2) naturalization extent (expressed as the number of GloNAF regions where the species occurs). In total, we found information on mycorrhizal type and status for 3211 naturalized plant species and 4200 non-naturalized plant species. Mycorrhizal plant species, both AM and ECM, were more likely to be naturalized and naturalized to a greater extent than NM plants. The effect of being an AM species was always stronger, with AM species having a greater naturalization extent than ECM species. Being the same mycorrhizal type or status, annual species were generally more likely to be naturalized than perennials. Species with facultative mycorrhizal associations were more successful than those with obligate mycorrhizal associations, but both groups tended to have a greater chance of being naturalized than NM species. These results indicate that being NM is generally less favorable for naturalization. Overall, our results confirm, at the global scale, those of regional studies that facultative association with AM provides plant species with a naturalization advantage. For the first time, we have shown that being mycorrhizal contributes not only to the size of the naturalized range, reflecting the ability to spread, but also to the ability to become naturalized in the first instance.

Key words: biological invasions; establishment; host–fungus relationships; invaded range size; mutualism.

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INTRODUCTION

A key stage in the process of plant invasion is the naturalization phase (Richardson and Pyšek 2012), which involves the establishment of self-sustaining populations in resident plant communities after anthropogenic introduction into a new region (Divíšek et al. 2018). This results in integration of alien species into local floras (Pyšek et al. 2012, 2017), once the species have overcome environmental and biotic barriers to reproduction (Richardson et al. 2000b, Blackburn et al. 2011). Success or failure in naturalization is driven by complex interactions of multiple factors including climatic matching between the native and introduced region, habitat legacy, propagule pressure (Lonsdale 1999), and species' biological and ecological traits (van Kleunen et al. 2015b, Pyšek et al. 2015). However, the role these factors play depends on the stage of invasion process and may differ for naturalized and invasive plants (Williamson 2006, Küster et al. 2008, Pyšek et al. 2009), that is, a subset of naturalized species that spread over large distances (Richardson et al. 2000b).

Despite the considerable attention paid to determinants of naturalization success, the role of mutualisms has received relatively less attention (Richardson et al. 2000a, Mitchell et al. 2006). One example is the relationship with mycorrhizal fungi. Although mycorrhizal symbiosis has been thoroughly studied in plant ecology, particularly since the seminal paper of Grime et al. (1987), in plant invasions it has been rather understudied. Recently, the rapid development of molecular techniques has improved our knowledge of these symbioses; biogeographic and taxonomic data are now available at a global scale (Öpik et al. 2010, Tedersoo et al. 2014, Pärtel et al. 2017). As a result, the role of mycorrhizal symbioses in plant invasions is becoming better understood (Delavaux et al. 2019, Steidinger et al. 2019).

Most mycorrhizal fungi exhibit low host specificity (van der Heijden et al. 2015), and arbuscular mycorrhizal (AM) fungi are generally widely distributed; some are even cosmopolitan (Davison et al. 2015). There is more specialization among ectomycorrhizae (ECM), as well as among mycoheterotrophic ericoid- and orchid-

mycorrhizal associations (Kennedy 2010, Pölme et al. 2018). Generally, however, there is a high probability that alien plant species, especially those with AM, will interact with mycorrhizal fungi not only in their native but also in their invaded range. The benefits of mycorrhizal fungi for the host plant are more efficient acquisition of water (Augé 2001) and nutrients, such as phosphorus, nitrogen, potassium, and zinc from the substrate (in exchange for photosynthates provided by the host plant; Smith and Read 1997), and protection of roots against pathogens (Vereşoglou and Rillig 2012). In addition, mycorrhizal fungi can mediate plant–plant interactions (Klironomos 2002, Callaway et al. 2004) and plant–herbivore interactions (Kempel et al. 2013), they can signal immediate threats to neighboring plants such as herbivores or pathogens (Gilbert and Johnson 2017), and they can affect other mutualistic partners of the host plant, including aboveground mutualists (Wolfe et al. 2005). Thus, mycorrhizal fungi can influence the performance of individual plant species and the composition of plant communities (van der Heijden et al. 1998, Klironomos et al. 2011).

Conceptual frameworks and meta-analyses (Pringle et al. 2009, Meisner et al. 2014) show how symbiotic fungi influence the success, failure, or trajectories of plant invasions. However, most studies assessing the role of mycorrhizal symbiosis in the plant invasion process have so far focused on the regional scale (Štajerová et al. 2009, Hempel et al. 2013, Bunn et al. 2015, Menzel et al. 2017, 2018, Reinhart et al. 2017), were based on a limited number of plant species (Callaway et al. 2004, 2008), or were conducted at the community level (Chęcinska Sielaff et al. 2019). Therefore, the effects of mycorrhizal associations on plant naturalization and invasion success at the global scale are still largely unknown. However, we can now assess how naturalization is related to mycorrhizal associations using the Global Naturalized Alien Flora (GloNAF) database, which is currently the most comprehensive compilation of naturalized alien floras, including data from over 1000 regional checklists across the globe (van Kleunen et al. 2015a, 2019, Pyšek et al. 2017). GloNAF includes data on naturalized plant species in both mainland and island regions, and has been used to study various

aspects of plant invasions at a global scale, providing robust tests of multiple invasion concepts and hypotheses (Seebens et al. 2015, Razanajatovo et al. 2016, Guo et al. 2018, 2019, Pyšek et al. 2019). Recently, Delavaux et al. (2019) used GloNAF data to perform a biogeographic study comparing naturalized alien floras in mainland vs. island regions and to infer colonization processes leading to current plant species distributions. The study revealed that the proportion of mycorrhizal plants in floras decreases from the equator toward the poles. In addition, members of naturalized floras on islands are more often mycorrhizal than naturalized species in mainland regions, a pattern attributed to the anthropogenic co-introduction of plants with their symbionts to islands and anthropogenic disturbance of symbionts on the mainland. Delavaux et al. (2019) suggested that mycorrhizal associations are an overlooked driver of global phyto-geographical patterns. It is therefore useful to explore this dataset further to study large-scale macroecological patterns of mycorrhizal associations among the world's naturalized plants.

To standardize studies of mycorrhizal associations in the global flora, Moora (2014) suggested distinguishing four mycorrhizal attributes of a plant species: (1) mycorrhizal status (obligate or facultative), (2) mycorrhizal type (arbuscular, ectomycorrhizal, ericoid, and orchid), (3) mycorrhizal flexibility, and (4) mycorrhizal dependency. The first two traits can provide insights into co-evolutionary processes underlying global patterns and ecological relationships between plants, mycorrhizal fungi, and the environment; however, the mechanisms behind these relationships remain largely unknown. To obtain information on the mycorrhizal status and type for hundreds to thousands of species, several databases have been collated: Harley and Harley (1987) for the British flora, Wang and Qiu (2006) with a global scope, Akhmetzhanova et al. (2012) for the former Soviet Union, and Hempel et al. (2013) and more recently Bueno et al. (2017) for Central Europe. Mycorrhizal flexibility (defined as plant species' ability to exist with or without mycorrhizal associations under given conditions) and mycorrhizal dependency (i.e., whether a plant species response to colonization by mycorrhizal fungi under different abiotic/biotic conditions is negative, neutral, or positive)

are also likely to be relevant for the invasion process. However, although such data are gradually accumulating (Chaudhary et al. 2016), they are still far too scarce to allow analysis of a large number of species.

Here, we tested whether the mycorrhizal status and type affect the global naturalization success of plant species. To this end, we combined information on the mycorrhizal type and status from the above-mentioned databases with information on species' distribution and biogeographical status from GloNAF (van Kleunen et al. 2015a, 2019, Pyšek et al. 2017). We measured naturalization success in two ways: (1) whether a species is recorded as naturalized anywhere in the world (naturalization incidence), and (2) if so, how widespread/successful it is (naturalization extent). This approach has been successfully used in previous studies testing the relationships between traits and global naturalization success, as it has revealed that factors related to likelihood of naturalizing *per se* may differ from those related to how widely naturalized a species is (Razanajatovo et al. 2016, Fenesi et al. 2019).

METHODS

Data

For each vascular plant species included in the mycorrhizal database, we acquired information on its mycorrhizal type and status. The classification into mycorrhizal types was based on the following types: AM, arbuscular mycorrhiza; ECM, ectomycorrhiza; ERM, ericoid mycorrhiza; and ORM, orchid mycorrhiza. For mycorrhizal status, we distinguished whether the mycorrhiza was obligate (OM) or facultative (FM). Non-mycorrhizal (NM) species were used for comparison against both mycorrhizal type and status.

The mycorrhizal associations were assigned based on two methods (cf. Bueno et al. 2019a). First, we applied the empirical approach to determine both the mycorrhizal type and status, by using (as of 2018) the most complete georeferenced mycorrhizal trait dataset for vascular plants (Bueno et al. 2017). These authors estimated vascular plant mycorrhizal traits by collecting and reviewing species-level information from large datasets of plant mycorrhizal information (Harley and Harley 1987, Wang and Qiu 2006, Akhmetzhanova et al. 2012, Hempel et al.

2013) and updated the list with an intensive literature search that added references to the empirical mycorrhizal information uncovered by the previous datasets. The core of the database used was checked for the effects of potential misclassification errors. An error rate of 20% did not change the mycorrhizal distribution pattern in Europe (Bueno et al. 2017).

Second, we applied a taxonomic approach to determine mycorrhizal types. This approach is based on an expert review of published information about mycorrhizal associations, and a further integration of this information with plant taxonomy. The ECM and ERM plant species are assigned mainly at the plant genus level (cf. Kohout 2017, Tedersoo and Brundrett 2017) and AM, NM, and FM plants at the plant family level (Brundrett 2017). Once plant families or genera were assigned, all unstudied species within those higher-order taxonomic groups were subsequently assigned to the same trait category. The taxonomic approach may result in incorrect assignments, especially in the case of the NM and FM categories (Bueno et al. 2019a, b). At the same time, the approach maximizes completeness of species coverage. We assigned mycorrhizal types to all species in the GloNAF dataset using the taxonomic approach.

The mycorrhizal trait data were combined with the GloNAF database (release 1.1), which provides information on the distribution of naturalized plant species in 843 regions (mostly at the scale of countries or smaller administrative units, such as states or provinces in the case of larger countries). The database includes 482 mainland regions and 361 islands (van Kleunen et al. 2015a, Pyšek et al. 2017). This version of the database included information on over 13,000 species introduced beyond their native range by human action and records of naturalization in the above regions. To be included in GloNAF, a species needs to be reported as naturalized (according to criteria of Richardson et al. 2000b, Blackburn et al. 2011) in at least one region of the world. Specifically, we determined (1) whether a species is capable of naturalization and hence is included in the GloNAF database (naturalization incidence), and for those that are, (2) in how many regions they occur (naturalization extent; as in Razanajatovo et al. 2016, Guo et al. 2018, Fenési et al. 2019). In total, there were 3211

naturalized species with information on mycorrhizal type and status in the empirical dataset and 13,791 naturalized species with information on mycorrhizal type in the taxonomic dataset; the 4200 non-naturalized species with information on mycorrhizal type and status were applicable to both datasets (see Fig. 1 and Appendix S1: Fig. S1 for the structure of the dataset and species numbers in particular categories and their combinations). Further, it is known that some life forms are more likely to have (or not have) mycorrhizal associations than others; to account for the interaction of the effects of mycorrhizal associations with life form, we used data on life form of each species (annual/biennial; perennial), taken from the GloNAF database and GIFT database (Weigelt et al. 2019).

Phylogeny

To account for phylogenetic relatedness of species, we constructed a species-level phylogeny using the dated supertree initially constructed by Zanne et al. (2014) and corrected and extended by Qian and Jin (2016). This tree includes 31,749 plant species and was generated based on several genetic markers. We pruned the supertree using the R function *S.PhyloMaker* (Qian and Jin 2016) to generate phylogenies for species used in our study. Species absent from the supertree were inserted as polytomies at the root node for their family or genera membership, following the approach implemented in *PhyloMatic* and *Bladj* (Webb et al. 2008).

Statistical analyses

All analyses were performed in R (R Core Team 2018). If a species was reported to occur in more than one mycorrhiza type or status category, it was assigned to each of them. The G test of goodness of fit was used to test whether the observed frequencies of each mycorrhizal type (both empirical and taxonomic data) in the GloNAF database were the same as those in the global flora reported by Brundrett (2017), that is, AM 78%, ECM 2%, ERM 2%, NM 8%, and ORM 10% of all species with known mycorrhizal types.

Due to very few species associated with ORM or ERM types in our datasets (125 ORM and 131 ERM in the empirical, and 184 ORM and 167 ERM in the taxonomic; Fig. 1 and Appendix S1:

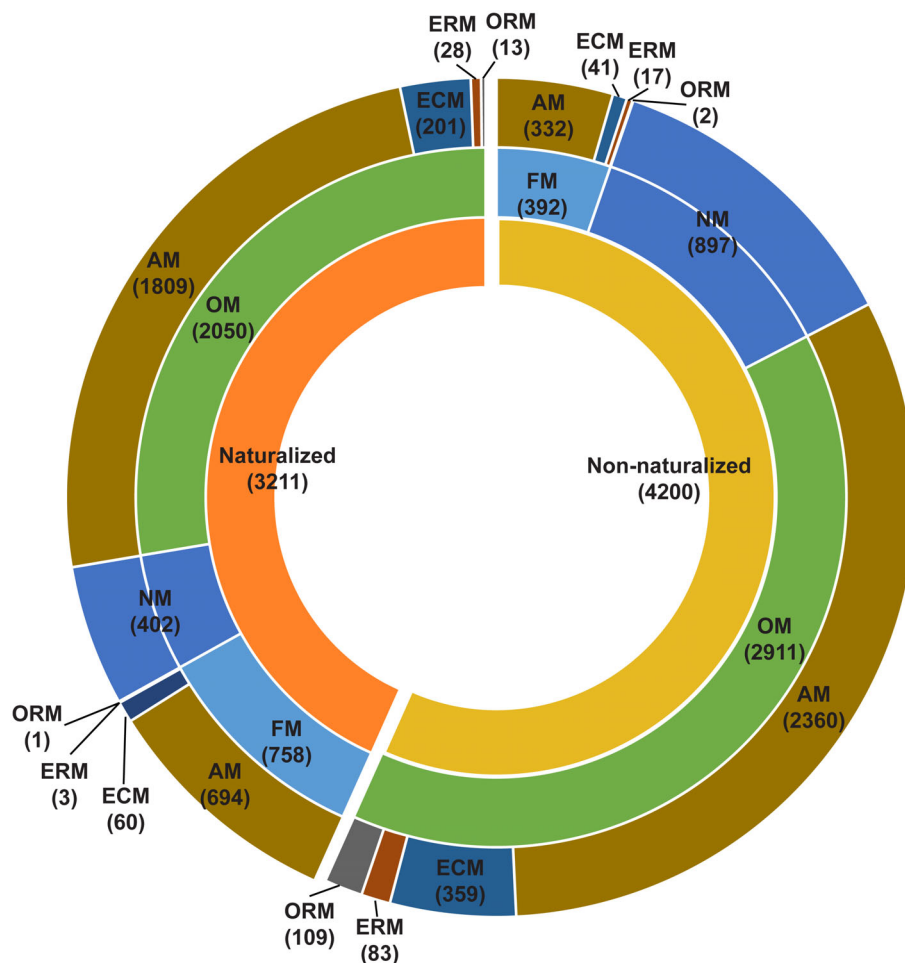


Fig. 1. Summary of species numbers used in the naturalization incidence analysis, based on the empirical approach. From interior to outward are groupings of naturalized/non-naturalized plant species, mycorrhizal status (facultative, obligate, and non-mycorrhizal), and mycorrhizal types (arbuscular, ectomycorrhizal, ericoid, orchid, and non-mycorrhizal; see *Methods* for explanation of abbreviations).

Fig. S1), these two mycorrhizal types were removed from the following mycorrhizal type analyses (i.e., both empirical and taxonomic data; Appendix S1: Figs. S2, S3). Species without life form information were also removed from the dataset (Appendix S1: Figs. S2, S3). Our data included hundreds of species showing variable life forms (Appendix S1: Table S1). Because of this, the previously reported effect of life form on naturalization incidence and extent (Guo et al. 2018), and the ambiguous effects of life form and mycorrhizal status on naturalization extent (Menzel et al. 2017), we ran the following analyses separately for each life form group, that is, annual/biennial and perennial. We used

phylogenetic logistic regression (Ives and Garland 2010), as implemented in the R package *phylolm* (Ho and Ane 2014), to analyze the relationships between naturalization incidence and either mycorrhizal type or mycorrhizal status, while accounting for phylogenetic relatedness. Similarly, we tested for the associations between naturalization extent and either mycorrhizal type or status using phylogenetic generalized linear regression in the *phylolm* package (Ho and Ane 2014), with naturalization extent log₁₀-transformed to improve the model normality. As our main aim was to test the effects of different mycorrhizal types/status on naturalization success, we relevelled mycorrhizal types/status and then

repeatedly ran the same models to obtain the pairwise differences.

Due to many infraspecific taxa in the taxonomic dataset, it was impossible to obtain a species-level phylogeny. Therefore, for the mycorrhizal type obtained from the taxonomic approach, we also ran generalized linear mixed-effects models (GLMMs) with a binomial error distribution (naturalization incidence model) or with a negative binomial error distribution (naturalization extent model) in the lme4 package (Bates et al. 2015), with genus nested within family as random factor to account for phylogenetic nonindependence of the species. As the main findings from both empirical and taxonomic data are largely similar, we show the results based on the empirical data in the main text and those of the taxonomic approach mainly in the supplementary material (Appendix S1).

RESULTS

Mycorrhizal associations in naturalized vs. global flora

For both the empirical and taxonomic datasets, the G tests of goodness of fit revealed significant differences between observed numbers, which reflect the frequencies of mycorrhizal types among naturalized plant species, and expected numbers, derived from the global flora based on Brundrett (2017; empirical— $G = 955.99$, $df = 4$, $P < 0.001$; taxonomic— $G = 3285.9$, $df = 4$, $P < 0.001$; Fig. 2 and Appendix S1: Fig. S4). In addition, post hoc tests between the expected and observed frequencies of mycorrhizal types also showed significant differences for most pairs of mycorrhizal types ($P < 0.001$, Fig. 2 and Appendix S1: Fig. S4). Species with the ECM type and NM species were significantly over-represented among naturalized species, while those with ERM and ORM were under-represented. In the empirical dataset, the observed number of plant species with the AM type was almost the same as the expected number (Fig. 2), but, in the taxonomic dataset, the AM-type plant species were significantly over-represented (Appendix S1: Fig. S4).

Naturalization incidence

The effects of the mycorrhizal type varied with life form. Arbuscular mycorrhizal plant species were more likely to be naturalized than NM

species, and the pattern was held for both annual/biennial species (that are generally more likely to be naturalized) and perennials. However, plant species with ECM type, which is only present among perennials, had lower naturalization incidence than both AM and NM plant species (Fig. 3a).

For the effect of mycorrhizal status on naturalization incidence (Fig. 3b), species with facultative mycorrhizas were more likely to become naturalized than those with obligate mycorrhizas, and non-mycorrhizal species had the lowest naturalization incidence. This pattern was consistent regardless of life form, even though the marginal effect varied slightly between life forms: Belonging to the same mycorrhizal status, annual/biennial species generally have higher chance to become naturalized than perennials.

The results based on the taxonomic approach differed from those based on the empirical dataset (cf. Fig. 3a with Appendix S1: Fig. S5). For the annual/biennial life form, the probability of being naturalized was similar for AM and NM species. For perennials, having the AM type significantly

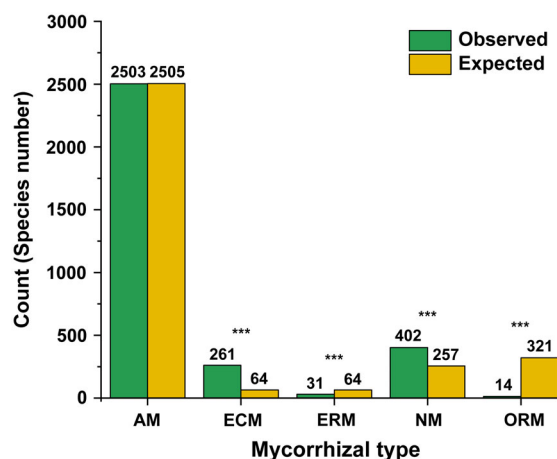


Fig. 2. Observed and expected frequencies of mycorrhizal types for the plant species in the Global Naturalized Alien Flora database, based on the empirical data (i.e., plant species with documented mycorrhizal type according to Bueno et al. 2017). Values above bars are the observed and expected number of plant species in each mycorrhizal type: AM, arbuscular; ECM, ectomycorrhizal; ERM, ericoid; ORM, orchid; NM, non-mycorrhizal. *** $P < 0.001$.

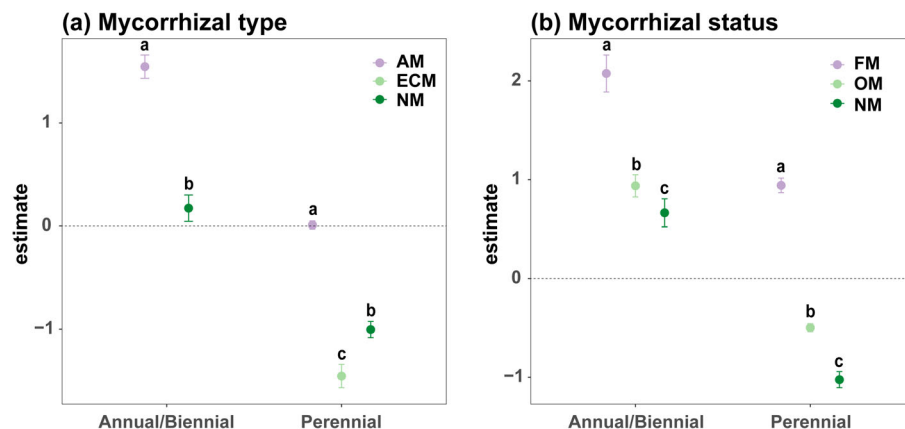


Fig. 3. Effects of mycorrhizal types (a) and status (b) on naturalization incidence. Estimates (log odds ratios of the probability of being naturalized) of the effects and the standard errors (bars) were extracted from each phylogenetic logistic regression model. Due to few annual/biennial species (5) associated with the ECM type, they were excluded in the mycorrhizal type analysis (a). Different letters in each model indicate significant differences between groups in the post hoc test ($P < 0.05$). Phylogenetic signals (α) for each model are shown in Appendix S1: Table S2. Mycorrhizal type: AM, arbuscular; ECM, ectomycorrhizal; NM, non-mycorrhizal. Mycorrhizal status: FM, facultative; OM, obligate; NM, non-mycorrhizal.

increased the probability of plants being naturalized compared to NM or ECM species.

Naturalization extent

Generally, analyses of the effect of mycorrhizal symbiosis on naturalization extent (Table 1) yielded similar results when we considered all regions, mainland regions (i.e., regions that are located on a continent), or islands separately. In terms of mycorrhizal type, both annual/biennial and perennial species with AM showed a significantly greater naturalization extent than non-mycorrhizal species (Fig. 4a). Perennial ECM species did not differ in naturalization extent from NM perennials but were significantly less widely naturalized than AM species on islands.

For annual/biennial life form, both facultative and obligate mycorrhizal species were naturalized in significantly more regions than non-mycorrhizal species. For perennials, species with facultative mycorrhiza had a significantly greater naturalization extent than both with obligate mycorrhiza and non-mycorrhizal species, which did not significantly differ from each other (Fig. 4b).

Using the taxonomic dataset, the GLMMs of mycorrhizal type (cf. Fig. 4a with Appendix S1: Fig. S7) provided similar results for annual/

biennial species, but for perennials, they differed in that the ECM species had a significantly greater naturalization extent than AM and NM globally and among mainland regions.

DISCUSSION

The majority of land plants are mycorrhizal (Smith and Read 2008, Brundrett 2017), but the influence of mycorrhizal symbiosis on plant species' ability to naturalize after introduction outside of their native range is still understudied. This is partly due to a lack of data until recently—the study by Delavaux et al. (2019) is an exception in this respect. Our present study differs from that of these authors in addressing the mycorrhizal associations at the plant species level, which allowed us to consider the effect of plants species' life history and phylogeny on the role of mycorrhizal symbiosis in facilitating invasion and in exploring naturalization likelihood and how widespread naturalized species are across regions. We also considered different mycorrhizal type and status.

In terms of mechanisms, it is still debated whether alien plants benefit from being mycorrhizal, or if being dependent on the symbiosis rather constrains their establishment and spread

Table 1. Summary of the naturalization extent (i.e., the number of Global Naturalized Alien Flora regions occupied) of species by mycorrhizal type and status

Type	No. of species	Min	Mean	Median	Max	SD	CV (%)	Species with		
								≤25 regions	≤50 regions	≤70 regions
(a) Mycorrhizal type: taxonomic approach										
AM	11,032	1	13.92	3	409	30.02	215.69	9364 (85%)		
ECM	534	1	10.01	3	154	17.16	171.49	473 (89%)		
ERM	70	1	3.29	2	26	4.06	123.59	69 (99%)		
NM	2082	1	11.12	2	249	22.94	206.27	1805 (87%)		
ORM	73	1	4.84	1	51	9.22	190.58	70 (96%)		
(b) Mycorrhizal type: empirical data										
AM	2776	1	32.9	10.5	409	49.10	149.38	2155 (78%)		
ECM	283	1	14.4	6	154	20.79	144.06	268 (95%)		
NM	429	1	23.8	8	249	36.77	154.62	362 (84%)		
(c) Mycorrhizal status: empirical data										
FM	863	1	43.07	17	311	58.34	135.43	676 (78%)		
OM	2197	1	26.48	8	409	41.57	156.97	1938 (88%)		
NM	429	1	23.78	8	249	36.77	154.62	387 (90%)		

Notes: AM, arbuscular mycorrhiza; ECM, ectomycorrhiza; ERM, ericoid mycorrhiza; FM, facultative mycorrhiza; NM, non-mycorrhiza; OM, obligate mycorrhiza; ORM, orchid mycorrhiza. (a) The mycorrhizal types were assigned using the taxonomic approach. (b) Empirical mycorrhizal type. (c) Empirical mycorrhizal status. For more details of the frequency distribution of the naturalization extents, see Appendix S1: Fig. S6.

into new regions (Richardson et al. 2000a, Pringle et al. 2009, Moora et al. 2011, Menzel et al. 2017). In our global study, mycorrhizal species, both AM and ECM, were more likely to be naturalized somewhere in the world than non-mycorrhizal species. It can be speculated that the high dispersal ability of AM (Davison et al. 2015) but to some extent also ECM fungi (Peay et al. 2012) could play a role here. In addition, many AM and ECM plant species with a high invasion potential may associate with a wide range of mycorrhizal fungi so finding an appropriate mutualistic partner when introduced to a new range is more likely (Richardson et al. 2000a). For example, the Douglas fir (*Pseudotsuga menziesii*; Pinaceae), native to western North America and naturalized in Europe, Argentina, Chile, and New Zealand where it is extensively planted for timber, can associate with more than 2000 ECM fungal species (Molina et al. 1992). For ECM, there is some evidence that co-introductions promote naturalizations of northern conifers in the Southern Hemisphere, but that introductions from North America to Europe involve recruitment of ECM fungi already present in Europe, which associate with similar native conifer species (Gundale et al. 2016). However, ECM fungi

are generally known to be rather host-specific compared to AM fungi (van der Heijden et al. 2015). There is also experimental evidence that alien species primarily associate with widely distributed generalist AM fungal taxa (Moora et al. 2011). In a recent study conducted in Texas, USA, at a plant community scale, alien grassland plant species had significantly higher colonization by AM fungi than native species, and this result was consistent across plant functional groups (Chęcinska Sielaff et al. 2019).

We also found that the effect of AM association was always stronger than for other mycorrhizal types, favoring a greater extent of naturalization than for ECM, while non-mycorrhizal species were the least widely naturalized. This suggests that being non-mycorrhizal is generally disadvantageous for alien plant success at a global scale (Richardson et al. 2000a, Pringle et al. 2009). Yet, there are some non-mycorrhizal species that are highly invasive under specific conditions such as European garlic mustard (*Alliaria petiolata*), which invades natural woodlands in North America (Callaway et al. 2008, Colautti et al. 2014). In addition, it is important to mention that there is a trade-off in associating with mycorrhizal fungi, because the association also

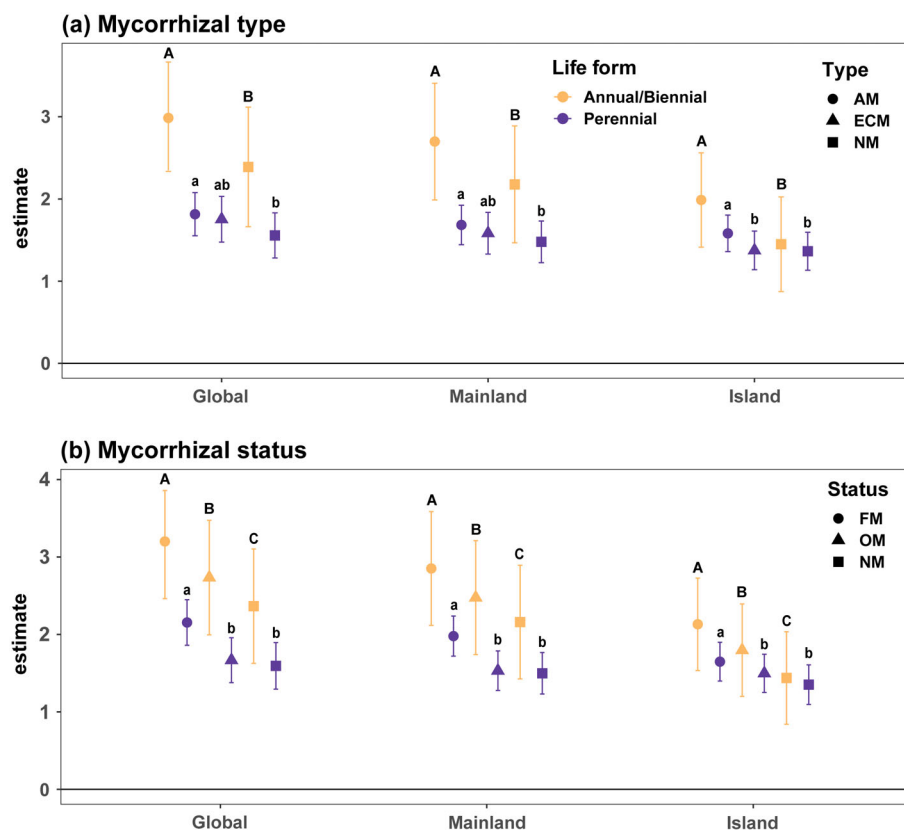


Fig. 4. Effects of mycorrhizal types (a) and status (b) on naturalization extent. Estimates of the effects and the standard errors (bars) were extracted from each phylogenetic generalized linear model regression model. As only few annual/biennial species (5) are associated with the ECM type, they were excluded from the mycorrhizal type analysis (a). Capital letters and lowercase letters indicate post hoc tests of annual/biennial and perennial models, respectively, and different letters in each model indicate significant difference between groups ($P < 0.05$). Phylogenetic signals (λ) for each model are shown in Appendix S1: Table S2. Mycorrhizal type: AM, arbuscular; ECM, ectomycorrhizal; NM, non-mycorrhizal. Mycorrhizal status: FM, facultative; OM, obligate; NM, non-mycorrhizal.

demands a considerable input from the plant partner (Hempel et al. 2013). The pattern described above, on the effect of AM associations, more or less holds regardless of life form, with the interaction suggesting that the positive effect of mycorrhizal association is more pronounced in annual species. Annuals are generally more likely to naturalize than perennials, and even non-mycorrhizal annual species rank higher in terms of naturalization success than AM perennials (Fig. 3a). This finding reflects the main characteristics of AM fungi, that is, being the most common and globally widespread type of mycorrhizal fungi and having a low host

specificity (Davison et al. 2015, Brundrett and Tedersoo 2018).

In terms of mycorrhizal status, plant species with facultative mycorrhizal associations appear to be most successful at being naturalized outside of their native range, more so than plants with obligate mycorrhizal associations, but both groups tend to have a higher probability of being naturalized than non-mycorrhizal species. Being a facultative mycorrhizal plant seems to be the best strategy when introduced to a new range as the naturalization process is not constrained by the availability of suitable fungal partners occurring in situ, and even the absence of mycorrhizal

fungi in the soil is not a large constraint—our paper provides robust empirical evidence for this phenomenon. Results similar to ours are reported at a regional scale by Hempel et al. (2013) who studied relationships between the occurrence of plant with various mycorrhizal associations, habitat characteristics, various plant traits, and patterns of plant distribution using the German flora. They found that facultative mycorrhizal plant species had a wider distributional range and broader ecological niche than species with other mycorrhizal status (see also Gerz et al. 2018). In another regional study, Gerz et al. (2018) found that facultative mycorrhizal plant species had the widest realized niches, in terms of both width and volume. At the lower taxonomic level, Dickie et al. (2010) showed that the lack of suitable mycorrhizal fungal species is a major constraint for invasions of pines (*Pinus* spp.) on islands.

Previous studies have tested the roles of mycorrhizal type and status in naturalization success at regional scales, albeit without distinguishing between different stages of invasion. Menzel et al. (2018) assessed the relationship between area of occupancy in Germany and two variables: plant species origin (natives; archaeophytes—alien species introduced before the year 1500; and neophytes—alien species introduced after the year 1500) and AM status (obligate, facultative, and non-mycorrhizal). They found that AM status significantly explained the area of occupancy of natives and neophytes, with facultative mycorrhizal plant species occupying larger areas in both groups—this corresponds to our finding reported above. These authors also showed that while in neophytes with facultative mycorrhizal associations there are trade-offs between plant retention of the mycorrhizal symbiosis and allocation of C to the development of other plant structures, such trade-offs were almost absent among natives (Menzel et al. 2018). This indicates that natives and neophytes benefit differently from mycorrhizal symbiosis and suggests that native AM fungal partners might be less important for neophytes than for native plant species, or that more time of co-evolutionary experience is required to establish similar relationships between neophytes and native fungal symbionts. In another regional study, Menzel et al.

(2017) reported that the mycorrhizal status significantly explained the occupied range of alien plants, with facultative mycorrhizal species inhabiting a larger range than non-mycorrhizal species, while obligate mycorrhizal plant species were intermediate. Moreover, aliens with storage organs, shoot metamorphoses, or specialized structures promoting vegetative dispersal were more widely distributed when being facultatively mycorrhizal. This mycorrhizal status is especially advantageous for successful spread of alien plants, as the flexibility of being facultatively mycorrhizal allows plants to explore a broader set of ecological strategies (Menzel et al. 2017).

In scaling up from these regional studies to our global one, we assume that facultative mycorrhizal plant species have a greater ability to colonize a wider range of habitats than obligate mycorrhizal and non-mycorrhizal plant species, and so are likely to have a larger naturalization extent. Indeed, when using the number of GloNAF regions as a measure of naturalization extent, our results support this assumption—overall mycorrhizal associations favored a wide distribution, but the effect was restricted to AM species, and as with naturalization incidence, facultative mycorrhiza was the most advantageous strategy for naturalization across a wide range of regions.

Overall, we show at the global scale that facultative AM plant species have the greatest advantage from mycorrhizal association, in that it favors their spread, resulting in a wide distribution. In addition, we show for the first time that AM association is not only related to how widespread naturalized plants are, but also to their ability to become naturalized at all, as illustrated by the effect of mycorrhizal type and status on the naturalization incidence. We are confident that the big picture we present here about the effects of mycorrhizal symbiosis on the plant species naturalization on the global scale is fairly robust, being based on unprecedented dataset for naturalized plants (Pyšek et al. 2017, van Kleunen et al. 2019). Although the data included in GloNAF vary in quality due to nonrandom global distribution of research efforts (van Kleunen et al. 2019), they represent the best available resource, covering a wide range of habitats, environments, and climates.

The importance of understanding the relationships between alien plants and their symbionts, including the extent to which the mycorrhizal symbiosis facilitates plant naturalization and spread, becomes even more urgent in light of results of some recent studies, showing that native and naturalized floras worldwide differ in their composition in conjunction with mycorrhizal association (Delavaux et al. 2019). In our study, we have found a link between the likelihood of a plant species being naturalized somewhere, and once naturalized how widespread it is globally, and its mycorrhizal association. This finding may be useful for forecasting global invasion risk, based on the mycorrhizal association of species that may not be introduced/naturalized outside of their native range yet. What we still need to understand is to what extent this link is due to fungal partners in question being widespread, or non-host-specific, or due to co-introductions. This opens a potentially promising venue for future research.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2937/full>

Appendix S1: Comparison with the results of the taxonomic approach